Limnol. Oceanogr., 55(4), 2010, 1485–1498

doi:10.4319/lo.2010.55.4.1485

Survival probability of larval sprat in response to decadal changes in diel vertical migration behavior and prey abundance in the Baltic Sea

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Abstract

We employed a coupled three-dimensional biophysical model to explore long-term inter- and intra-annual variability in the survival of sprat larvae in the Bornholm Basin, a major sprat spawning area in the Baltic Sea. Model scenarios incorporated observed decadal changes in larval diel vertical distribution and climate-driven abiotic and biotic environmental factors including variability in the abundance of different, key prey species (calanoid copepods) as well as seasonal changes, long-term trends, and spatial differences in water temperature. Climate forcing affected Baltic sprat larval survival both directly (via changes in temperature) and indirectly (via changes in prey populations). By incorporating observed changes in larval diel vertical migration, decadal changes in modeled and observed survival of Baltic sprat agreed well. Higher larval survival (spawning stock biomass) was predicted in the 1990s compared to the 1980s. After changing their foraging strategy by shifting from mid-depth, low prey environment to near-surface waters, first-feeding larvae encountered much higher rates of prey encounter and almost optimal feeding conditions and had a much higher growth potential. Consequently, larvae were predicted to experience optimal conditions to ensure higher survival throughout the later larval and early juvenile stages. However, this behavioral shift also increased the susceptibility of larvae to unfavorable wind-driven surface currents, contributing to the marked increase in interannual variability in recruitment observed during the past decade.

The Baltic Sea ecosystem has undergone a dramatic regime shift from a cod-dominated system in the 1980s to a sprat-dominated system today (Köster et al. 2003; Casini et al. 2009; Möllmann et al. 2009). Climate-driven environmental changes that favored this shift included a reduction in salinity and oxygen conditions and an increase in water temperature. The dramatic decline of cod (an outcome of both environmental change and anthropogenic activities) resulted in dramatic, cascading effects on the Baltic food web (Casini et al. 2009; Möllmann et al. 2009). Responses in lower trophic levels include changes in the species composition of the zooplankton community of the Central Baltic. In terms of dominant copepod species, *Pseudocalanus acuspes* requires high salinity (Vuorinen et al. 1998) and low summer water temperatures (Möllmann et al. 2000) and has dramatically declined during the past decade. In contrast, *Temora longicornis* and *Acartia* spp. benefit from higher water temperatures and lower salinities in spring (Möllmann et al. 2000) and have increased during the same period. Changes in the standing stocks of these different calanoid copepods due to climatic factors may have been reinforced (or amplified) by changes in top-down control of zooplankton by plantivorous fishes. For example, Möllmann et al. (2008) reported that predation pressure by juvenile and adult sprat can markedly reduce standing stocks of *P. acuspes* but have little effect on *T. longicornis* and negligible effects on *Acartia* spp. In contrast to adults, larval sprat prey on all nauplii stages of four copepods—*P. acuspes*, *Acartia* spp., *T. longicornis*, and *Centropages hamatus*—and, at larger sizes, feed on all copepodite and adult stages of the latter three species (Dickmann et al. 2006). Changes in the abundance of these copepod species had pronounced effects not only on the composition but also on the depth distribution of potential larval sprat prey. All life stages of *Acartia* spp. dwell in the uppermost water layers along with the earliest stages of *P. acuspes* (Schmidt 2006), but more advanced stages of *P. acuspes* dwell in deeper waters. Thus, the potential prey field for sprat in deeper waters has been substantially reduced in recent years (Schmidt 2006).

Oxygen content and salinity have been shown to be the major environmental factors affecting the Baltic cod egg fertilization and survival rates (Wieland and Zuzarte 1991), and indirectly by determining the vertical overlap of cod eggs and their clupeid predators (Köster et al. 2001). The principal mechanism influencing the replenishment of oxygen in the deep basins of the Baltic is the inflow of saline oxygen-rich waters from the North Sea. During the longest recorded period without a major Baltic inflow of North Sea water (1977–1993), oxygen and salinity concentration in the deep basins of the Baltic were dramatically reduced.

Sprat is both an important prey species for cod and an important predator species on cod eggs and lower trophic levels (Möllmann and Köster 2002). The corresponding decrease in predation pressure by cod on sprat, combined with low fishing mortality and high reproductive success of the latter species, resulted in this pronounced increase of the sprat stock (Parmanne et al. 1994). Previous studies have found significant but weak correlations between sprat

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recruitment strength and spawning stock biomass and temperature conditions experienced during the egg and early larval stages of Baltic sprat (Köster et al. 2003). However, Köster et al. (2003) noted that estimates of egg and larval abundance were generally well correlated, whereas larval production poorly predicts recruitment levels. Thus, it has been argued that year-class strength in Baltic sprat may rather be determined by the influence of environmental factors acting during the late larval and early juvenile stages (Voss et al. 2006). The latter was supported by strong correlations between long-term changes in the drift trajectories of sprat larvae, estimated from Lagrangian particle-tracking simulations and sprat recruitment (Baumann et al. 2006). A drift index was utilized that likely reflected the variable degree of annual and seasonal larval transport from the central, deep major spawning basins (Arkona Basin, Bornholm Basin, Gdansk Deep, and Gotland Basin) to the shallow coastal areas of the Baltic Sea. The drift index was significantly correlated to sprat recruitment success and explained, together with sprat spawning biomass, 82% of the overall variability between 1979 and 2003. Years of strong larval displacement toward coastal regions corresponded to relative recruitment failure, while years of retention within the deep basins were associated with relative recruitment success. However, the biological mechanisms underlying these strong correlations need to be better resolved.

Density-dependent processes operating during the late larval and early juvenile stages in marine fish can substantially modify recruitment levels (Leggett and Deblois 1994). Results of drift simulations predicted much higher aggregations of larvae during years of large-scale coastal transport compared to years characterized by retention of larvae within deep spawning basins with the strength of aggregation (particle concentration) significantly inversely related to recruitment strength from 1991 to 2003. The fact that such a relationship was apparent only throughout the past decade may be explained by the, on average, higher larval abundance during the 1990s (Baumann et al. 2006). The strong increase of the sprat spawning stock at the end of the 1980s may have increased the effect of transport-related, density-dependent processes. Although the observed range of coastward-oriented transport rates or retention periods of larval sprat was similar, the magnitude of recruitment fluctuations almost doubled from the 1980s to the 1990s. Even though the strong increase in spawning stock biomass may have been the most important factor responsible for the shift in the drift-recruitment relationship, it co-occurred with a whole suite of changes in the Baltic Sea ecosystem (Möllmann et al. 2009). Particularly, it is unknown to what extent prey field dynamics such as pronounced shifts in the composition of Baltic zooplankton (Möllmann et al. 2000) contributed to decadal changes in recruitment variability.

The vertical distribution of feeding Baltic sprat larvae obtained from vertically resolved sampling performed during the late 1980s indicated diurnal vertical migration patterns, with the majority of larval sprat concentrated in uppermost, mixed surface water masses during the night (nonfeeding period) and at mid-depth during daytime (the main feeding period; Voss et al. 2003). This vertical distribution pattern was not in accordance with most recent vertically resolved measurements, indicating that larvae occurred almost exclusively in the upper water masses throughout the day and night (Voss et al. 2003). This substantial change in vertical distribution and hence in feeding ecology of Baltic sprat larvae, which must have taken place between the late 1980s and early 2000s, coincided with the previously described changes in zooplankton composition and abundance. Since Baltic sprat larvae exclusively occurred in higher levels of prey abundance in the upper water layers compared to lower prey abundances at mid-depth, an increase in larval survival seemed to be very likely.

In terms of explaining observed life history strategies and patterns of spatial (depth) distribution of sprat early life stages in the Baltic, we consider the effect of bottom-up processes (e.g., prey dynamics) on growth and survival to be more important than top-down processes (e.g., predation pressure). In this species-poor system, predation is unlikely to be a driving factor for a selection process acting on larval fish because of a relatively low encounter rate between piscivores and their prey (Köster et al. 2001). From a fitness perspective, larval fish should avoid habitats (e.g., water depths) that increase the probability of encounters with predators. Vikebø et al. (2007) modeled larval depth selection based on an inherent trade-off rule between growth (prey abundance) and mortality (predator contact). In most marine systems, the main potential predators of larval fish are planktivorous fish (Bailey and Houde 1989). In the Baltic Sea, herring (*Clupea harengus*) and sprat are the most abundant, potential larval fish predators that have been shown to prey on larval fish in the laboratory (Fuiman and Gamble 1988). However, field data indicate that in the Baltic, these species consume predominantly zooplankton (Möllmann and Köster 1999). Invertebrates may also prey on fish larvae, although no evidence of such predation has been found in the Baltic Sea ecosystem (e.g., from an analysis *Aurelia aurita* gut contents; STORE 2003; Barz and Hirche 2005). Haslob et al. (2007) could not find any evidence for predatory effects of the new invasive ctenophore *Mnemiopsis leidyi* on larval fish in the Bornholm Basin. The low degree of fish and invertebrate predation on larval fish in the Baltic Sea likely results from little vertical overlap between predators and prey (Köster et al. 2001).

The main purpose of this study was to use a new approach to investigate the causes and consequences of an observed change in the vertical distribution pattern or vertical migration behavior of Baltic larval sprat in light of historical, climate-driven changes in key environmental factors. The survival of larval sprat cohorts originating from a main spawning area (the Bornholm Basin) was examined using model scenarios that incorporated observed, decadal changes in larval vertical distribution and climate-driven abiotic and biotic environmental factors. The latter included variability in the abundance of different, important prey species (calanoid copepods) as well as seasonal changes, long-term trends, and spatial differences in water temperature. Using this approach, we

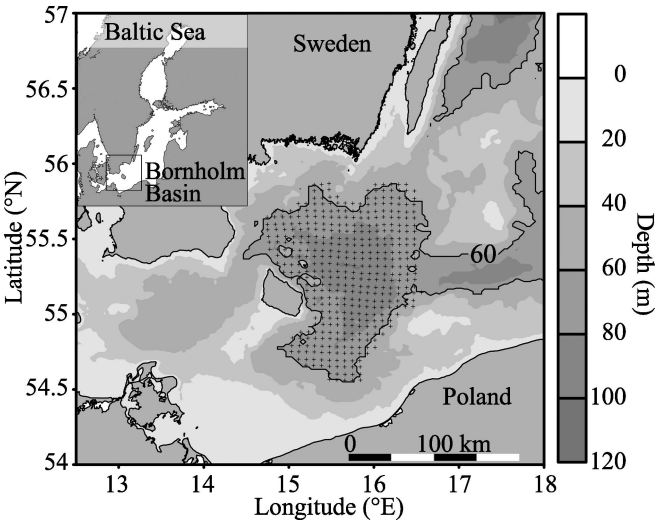

Fig. 1. Map of the Bornholm Basin indicating the seeding positions of Lagrangian drifters used in the hydrodynamic circulation model (small dots).

attempt to disentangle the roles of various extrinsic abiotic and biotic factors (ocean circulation, ambient temperature, shifts in prey composition and abundance) and intrinsic factors (changes in larval behavior) affecting larval sprat growth and survival. Based on this process knowledge, we hope to shed light on the mechanisms responsible for the long-term (decadal) dynamics of recruitment in the Baltic sprat stock.

Methods

Although four major sprat spawning areas exist in the Baltic Sea (Arkona Basin, Bornholm Basin, Gdansk Deep, and Gotland Basin), our analysis is restricted to the Bornholm Basin (Fig. 1). This was due to (1) the high availability of environmental time-series data for this specific spawning area, (2) the fact that most of the knowledge on larval feeding ecology implemented within our individual-based model (IBM) on larval growth and survival was obtained from larvae that were spawned in the Bornholm Basin, and (3) the lack of specific knowledge on vertical distribution and migration behavior of larval sprat in the other spawning areas.

Hydrodynamic model and particle tracking—The hydrodynamic model is based on the free surface Bryan–Cox–Semtner model (Killworth et al. 1991), which is a special version of the Cox numerical ocean general circulation model (Bryan 1969). A detailed description of the equations and modifications made, necessary to adapt the model to the Baltic Sea, can be found in Lehmann and Hinrichsen (2000). A detailed analysis of the Baltic Sea circulation has been performed by Lehmann et al. (2002).

The model domain comprises the entire Baltic Sea including the Gulf of Bothnia, the Gulf of Finland, and the Gulf of Riga, as well as the Belt Sea, Kattegat, and Skagerrak. The horizontal resolution is 5 km, with 60 vertical levels specified. The thickness of the different levels is chosen to best account for the different sill depths in the Baltic. The Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (Norrköping, Sweden) and river runoff taken from a mean runoff database. The meteorological database covers the whole Baltic Sea drainage basin with a grid of $1^\circ \times 1^\circ$ squares. Meteorological parameters, such as geostrophic wind, 2-m air temperature, 2-m relative humidity, surface pressure, cloudiness, and precipitation, are stored with a temporal increment of 3 h. Prognostic variables of the model are the baroclinic current field, the three-dimensional temperature and salinity distributions, the two dimensional surface elevations, and the barotropic transport (Table 1). Physical properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (Lehmann and Hinrichsen 2000).

Simulated three-dimensional velocity fields were extracted (at 6-h intervals) in order to develop a database for a Lagrangian particle-tracking exercise for larval sprat. This data set offers the possibility to derive Lagrangian drift routes by calculating the advection of ''marked'' water particles. Vertical velocities were calculated from the divergence of the horizontal velocity fields. The drifters were allowed to leave the layers where they were launched. The positions of the drifters varied over time as a result of the three-dimensional velocities that they experienced. Furthermore, the database contains information on the temperatures experienced along the drift routes required for simulating temperature-dependent processes affecting larvae (described below). In order to establish a Lagrangian view of the simulated circulation, drifters can be placed in the modeled flow fields at every location within the model domain. Moreover, the initial launch positions can be chosen independently from the vertical resolution of the model's grid. Simulated drift routes were obtained from Eulerian flow fields by utilization of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated drifters were computed using a fourth-order Runge–Kutta scheme.

Trophodynamic model—The IBM used in this study is described in detail by Daewel et al. (2008). Some of the parameter estimates were derived from laboratory studies on larval Atlantic herring *Clupea harengus* (metabolism and functional forms of prey capture success) and field data on larval sprat (growth rates and gut contents). Only the main features of the foraging and growth calculations are presented here. Larval growth rate (G, μg dry weight d^{-1}) was calculated as the difference between net dry weight (dry wt) of consumed food and metabolic losses:

$$G = C \cdot AE \cdot (1 - R_{SDA}) - R \quad (1)$$

where the rate of consumed prey (C, μg dry wt d^{-1}) was reduced by an assimilation efficiency (AE, %) and metabolic losses (R, μg dry wt d^{-1}), which were divided into several components to account for standard (R_S), feeding (specific dynamic action, R_{SDA}), and active (R_A) rates of energy loss. In Eq. 1, R represented R_S at night and

Table 1. Description of meteorological and hydrodynamic model parameters.

Variable	Unit	Area	Temporal resolution	Source
Meteorological database				
Geostrophic wind	m s^{-1}	Baltic Sea	3 hourly	SMHI
2-m air temperature	°C	Baltic Sea	3 hourly	SMHI
2-m relative humidity		Baltic Sea	3 hourly	SMHI
Sea surface pressure	hPa	Baltic Sea	3 hourly	SMHI
Cloudiness		Baltic Sea	3 hourly	SMHI
Precipitation	m s^{-1}	Baltic Sea	3 hourly	SMHI
River runoff	km^3 $month^{-1}$	Baltic Sea	Monthly	SMHI
Hydrodynamic model				
Ocean currents	m s^{-1}	Baltic Sea	5 min	Model
3-D temperature	°C	Baltic Sea	5 min	Model
3-D salinity		Baltic Sea	5 min	Model
2-D sea surface elevation	m	Baltic Sea	5 min	Model
Barotropic transport	m s^{-1}	Baltic Sea	5 min	Model

R_A during daylight foraging hours. Effects of larval dry weight and temperature on R were taken from experimental laboratory work on larval herring (Kiørboe et al. 1987). The amount of prey consumed was calculated as a function of encounter rate, prey mass, capture success, and handling time (Letcher et al. 1996). Prey encounter depends on a larva's search volume and its prey concentration, while capture success depends on prey length and larval standard length (SL) and was calculated using a formula reported by Munk (1992) modified to represent changes in prey sizes found within gut contents of 10–20-mm SL larval sprat. The handling time was calculated following an empirically derived equation from Walton et al. (1992) but reparameterized using field data on larval sprat gut contents (Dickmann et al. 2006). Overfeeding by larvae was eliminated by employing a C_{MAX} function:

$$C_{MAX} = 1.315 \cdot \text{dry wt}^{0.83} \cdot 2.872^{\left[\frac{(T-15)}{10}\right]} \quad (2)$$

yielding larval dry weight- and temperature (T, °C)-specific limits to food consumption rate (μg dry wt of prey d^{-1}) that balanced in situ estimates of dry weight- and T-specific sprat growth (Ré and Gonçalves 1993). In the model, G was partitioned between dry weight (μg) and SL (mm) depending on the condition factor (Φ):

$$\Phi = 1000 \cdot \frac{\text{dry wt}}{\text{SL}^{5.022}} \quad (3)$$

If growth in dry weight was positive and if $\Phi \geq 1.0$, SL increased according to equations provided by Peck et al. (2005). If growth in dry weight was continuously negative, the larva died (was removed from the simulation) when $\Phi < 0.75$.

Long-term temperature evolution—Temperature data in the Baltic Sea were compiled from the International Council for the Exploration of the Sea (ICES) Oceanographic Database containing depth-specific conductivity–temperature–depth and bottle measurements. From the database, we selected all available temperature profiles between the middle of the 1970s and 2002 within the Bornholm Basin. Data were subsequently aggregated to obtain monthly means per year and 5-m depth stratum down to 90 m.

Constructed prey fields—Depending on their size, larval sprat eat all nauplii stages of four copepods—*P. acuspes*, *Acartia* spp., *T. longicornis*, and *C. hamatus*—and all copepodite stages of the latter three species (Dickmann et al. 2006). The biomass and abundance of these major mesozooplankton species in the Central Baltic Sea (including data from the Bornholm Basin) were obtained from a database of the Latvian Fish Resources Agency (LATFRA). Sampling was performed on various stations in discrete depth strata from 0 to 25, 25 to 50, and 50 to 100 m. The data were derived from numerous surveys during the period 1959–1997 (Table 2). Detailed descriptions of the database as well as sampling and analysis procedures were provided by Möllmann et al. (2000). At each sampling station, concentrations of suitable copepod nauplii and all copepodite stages (including adults) were combined to represent prey fields for different larval size classes and assigned to bottom depths and day of the year. These different prey types found in the diet of sprat larvae were converted to dry weight using the formula by Hernroth (1985). Data aggregated from the whole central Baltic Sea were used here as a proxy for larval feeding conditions in the Bornholm Basin. To obtain a spatiotemporal resolution of the prey field, the zooplankton abundances from all stations covered in the central Baltic Sea were fitted to a second-order polynomial function. Hinrichsen et al. (2002) provided details on the construction of these temporally and spatially resolved prey fields.

Model scenario runs—The modeling approach employed here is based on a combination of the hydrodynamic model of the Baltic Sea (Lehmann and Hinrichsen 2000) and the IBM for larval sprat described in previous sections. A critical point regarding this type of modeling is that only passive sprat life stages could be examined. The swimming ability of marine fish larvae increases with increasing larval length (Peck et al. 2006), and schools of sprat are observed

Table 2. Description of prey field time series used in the individual-based model on feeding, growth, and survival of Baltic larval sprat.

Variable	Unit	Area	Season	Source
Acartia spp.	kg m^{-3}	Central Baltic	Spring	LATFRA
Acartia spp.	kg m^{-3}	Central Baltic	Summer	LATFRA
Centropages hamatus	kg m^{-3}	Central Baltic	Spring	LATFRA
C. hamatus	kg m^{-3}	Central Baltic	Summer	LATFRA
Temora longicornis	kg m^{-3}	Central Baltic	Spring	LATFRA
T. longicornis	kg m^{-3}	Central Baltic	Summer	LATFRA
Pseudocalanus acuspes	kg m^{-3}	Central Baltic	Spring	LATFRA
P. acuspes	kg m^{-3}	Central Baltic	Summer	LATFRA

at body sizes of 18 mm SL, indicating a capacity for swimming ability to exceed prevailing current velocities and alter drift routes at that size. Moreover, at this body size, sprat enters a (postlarval) life stage where many correlations (e.g., between distribution and environmental parameters) either break down or become difficult to examine (because of a lack of field data). In our approach, we have tracked individual larvae through the model domain as they potentially grew from 8 to 18 mm SL. This size range included (1) a sufficient drift duration, (2) only the period of established feeding on mesozooplankton and not yolk sac or microzooplankton feeders, and (3) larvae that make small foraging movements (e.g., vertical migration) but can still be considered passive drifters. Simulations started with different initial larval sizes (8, 9, and 10 mm), all of which select mesozooplankton stages as prey.

The hydrodynamic model was utilized to simulate Baltic sprat larval drift for the time period 1979–2002 and provided a database that was coupled to the sprat IBM calculating foraging, growth, and survival using a 6-h time step (Daewel et al. 2008). Temperatures required for the calculation of larval sprat growth rates along their drift routes were provided by the hydrodynamic model. A total of 424 drifters was released per run within the Bornholm Basin. The initial horizontal release locations were derived from mean distribution maps of advanced developmental stages of sprat eggs (A. Makarchouk pers. comm., LATFRA), assumed to be a proxy for the distribution of first feeding larvae. Accordingly, larval drifters were released on a regularly spaced grid ($\sim$ 5-km resolution) enclosed by the 40-m isobath representing the main spawning area of the Bornholm Basin (Fig. 1). Nine cohorts of larval drifters, at their release representing feeding larvae, were inserted into the modeled flow fields at 10-d intervals from 21 April through 10 July and were tracked until the larvae reached a size of 18 mm SL. The release dates encompassed the spawning period of eastern Baltic sprat (Table 3). The primary source of information on the timing of spawning was derived from unpublished information (A. Makarchouk pers. comm., LATFRA). While most of the spawning occurs in the deeper part of the basins (Nissling et al. 2003), feeding larvae are in recent years found mainly in the upper part of the water column. In a first approach, sprat larvae were released as Lagrangian drifters and forced to remain at depth between 5 and 10 m (depths at which feeding larvae occur after their initial ontogenetic vertical feeding migration). This is in accordance with recent field observations (Voss et al. 2007) showing no diel differences in vertical distribution since the early 1990s.

In a second approach, sprat larvae were assumed to actively change their vertical position in the water column, potentially altering their drift routes. Sprat larvae are visual feeders, and their vertical movements are probably associated with a diel feeding periodicity. Evidence for such behavior is presented by Voss et al. (2007), who observed diel vertical migrations of sprat larvae during the late 1980s: larvae concentrated at mid-depths during day but migrated vertically in an upward direction during nighttime. To account for differences in larval transport due to this vertical migration behavior, a second model was set up by assigning a simplified behavior to particles: larvae were assumed to be in the depth range of 5–10 m for 12 h per day and between 30 and 40 m for the other 12 h. This highly simplified scheme captured the essential features of the behavior and depth of occurrence of feeding larvae.

In order to account for the temporal evolution of the mesozooplankton composition and concentrations, several combinations of prey abundance scenarios and vertical migration patterns were tested. Thus, we successively modified the simulations by considering mean, high (mean + 50%), and low (mean − 50%) prey field concentrations (Table 4). The output results obtained from the different scenario runs are given as relative survival rates of larval cohorts at sizes of 18 mm SL. In order to account for the long-term changes in the abundance and composition of the zooplankton assemblage as well as for the expected changes in larval behavior, we calculated a sixth scenario that is a composite of the results obtained for the scenario

Table 3. Release dates for larval cohorts.

Cohort	Release date	Day of the year
1	21 Apr	110
2	01 May	120
3	11 May	130
4	21 May	140
5	31 May	150
6	10 Jun	160
7	20 Jun	170
8	30 Jun	180
9	10 Jul	190

Table 4. Combinations of diurnal vertical migration (DVM) and relative prey abundance (%) for scenarios 1–5.

		Relative prey abundance	
	DVM	*Pseudocalanus acuspes*	*Acartia* spp., *Temora longicornis*, *Centropages hamatus*
Scenario 1	Yes	150	100
Scenario 2	Yes	100	100
Scenario 3	Yes	50	100
Scenario 4	No	50	100
Scenario 5	No	50	150

runs 1, 2, 4, and 5. For the earliest period (1979–1983), when the abundance of *P. acuspes* was relatively high, the results of scenario 1 were used, followed by results from scenario 2 for the period 1984–1988 (when *P. acuspes* was declining). For the years 1989–1994, we expected a change in the vertical migration behavior of the larvae; thus, the results of the scenario 4 were included. Finally, in response to the strong increase in *Acartia* spp. abundance, results of scenario 5 were used for the last part of the modeling period (1995–2002).

Because of the lack of highly spatially and temporally resolved prey fields, we were unable to perform model experiments exploring more complex interactions between larval fish and their prey fields. For example, it was not possible to investigate how specific behavioral and physiological differences among larvae (e.g., interindividual differences in swimming speed and/or prey capture success) or behavioral adaptations of zooplankton to predation (e.g., terms of vertical migration) might influence prey encounter, larval feeding, growth, and survival. For example, Munk and Kiørboe (1985) reported that larval herring altered their swimming speed after encountering prey, thus increasing the probability of retention within a prey patch.

Results

Long-term temperature evolution—Figure 2 shows the spring (April–June) temperature evolution for the Bornholm Basin for the period 1976–2002, based on monthly mean values obtained from the ICES hydrographic database. Down to about 50–60 m, the seasonal mixed layer development can be observed. In contrast to the upper mixed layer, temperature changes within and below the halocline are due to variability in the advective inflows of water from the western Baltic and the North Sea. For near–sea surface waters (0–20 m), a large seasonal and interannual variability exists with an increasing trend of about 0.5°C decade^{-1}. A similar but less pronounced trend was observed for the lower mixed layer (20–40 m). The trend was dominated by a temperature increase in summer and autumn, while a slightly negative trend was observed during the winter.

Long-term zooplankton evolution—Nonseasonal biomass anomalies of *P. acuspes* in the central Baltic were variable until the beginning of the 1970s followed by a positive phase until the middle of the 1980s. Afterward, nonseasonal biomass anomalies markedly declined to very low

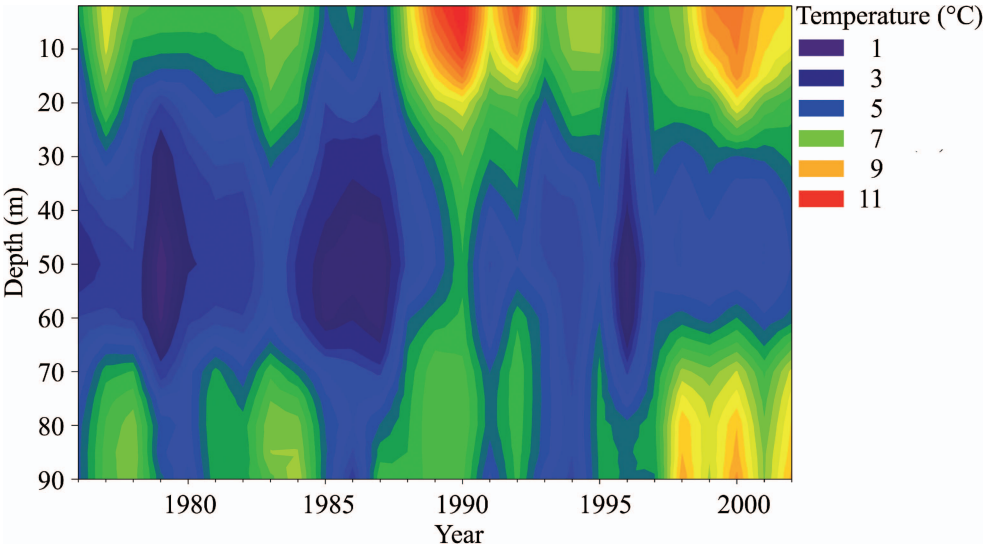

Fig. 2. Depth-specific temperature time series of the Bornholm Basin, Baltic Sea, obtained from ICES hydrographic database (*see* text for details).

levels in the middle of the 1990s. During the most recent years, biomass anomalies were still negative but slightly higher. Clear trends were also observed for *Acartia* spp., where negative anomalies dominated from the 1960s to the end of the 1970s, after which anomalies slightly increased during the 1980s. The most obvious feature in the biomass development of *Acartia* spp. was the mostly positive anomalies observed during the 1990s.

Model scenario runs—Generally, varying temperature and prey field composition and biomass affected the survival of only the smallest (8 mm) Baltic sprat larvae employed within these simulations. All scenario runs revealed optimal feeding conditions for sprat larvae that were $>$ 8 mm SL (i.e., in situ concentrations of suitably sized prey were always above survival thresholds for 9- and 10-mm initial SL larvae). Scenario 1 provided results according to larval feeding conditions observed during the late 1970s and early 1980s (Fig. 3A). The larvae were allowed to migrate vertically and were concentrated at mid-depths during day but migrated upward during nighttime. The availability of high prey concentrations of *P. acuspes* (150%) and only average biomasses of *Acartia* spp. (100%) yielded relatively high survival rates of the larvae, especially early in the season, but high interannual variability of larval survival for cohorts that were initially released relatively late in the season.

A shift in ambient temperature and in the feeding environment was observed during the second half of the 1980s (scenario 2, with diurnal vertical migration). Temperatures in the larval habitat increased by 2°C in some cases, and the copepod biomasses showed average conditions (100%) for both *P. acuspes* and *Acartia* spp. Generally, the survivorship of Baltic sprat larvae drastically changed in response to these new environmental conditions. Throughout the entire time series, larval survival was in the range of only 0–10% and only occasionally reached values up to 22.4% (Fig. 3B). Extremely poor conditions for growth and survival existed for larvae experiencing environmental conditions represented by scenario 3, that is, including diurnal vertical migration and low *P. acuspes* (50%) and average *Acartia* spp. (100%) biomasses (Fig. 3C). This extreme growth condition might have prevailed during the late 1980s and the beginning of the 1990s. Remaining on the same feeding level and allowing the larvae to remain only in the upper water layers (scenario 4) led to higher survival probability throughout the entire time series (Fig. 3D) but also yielded high intra- and interannual variability in survival. Hence, a sudden change in vertical behavioral migration of the larvae, as suggested from observational data, could have led to this considerable shift in survivorship. Accounting for the observed increase in *Acartia* spp. (150%) biomass since the middle of the 1990s and only low abundance of *P. acuspes* (50%; scenario 5) resulted in almost optimal growth conditions and hence in almost 100% survivorship of the larvae (Fig. 3E). Estimates of larval survival in the composite scenario (6) were low to moderate from 1984 to 1994 but extremely high (nearly 100%) at the beginning (1979–1983) and final (1995–2002) phases of the simulation because of high abundances of *P. acuspes* and *Acartia* spp. in the former and latter periods, respectively (Fig. 3F).

Spatial patterns in larval survival were noted within the release area (Bornholm Basin), and those patterns changed during different time periods in scenario 6 (Fig. 4). For most of time periods, survival success was highest for larvae that started first feeding within the deep basins (Fig. 4A,C,D). However, during most of the recent years (1995–2002), survival was relatively high (0.8) in the center area of the Bornholm Basin but was considerably lower in that region (0.3–0.6) during the first 4 yr examined (1979–1983). Temporal differences in survival were also apparent at the outer edges of the deep basin, where the highest survival probabilities (0.2–0.6) were obtained for the most recent years and relatively low survival was predicted during earlier time periods (Fig. 4A,C). No clear spatial patterns in larval survival were evident for the time period between 1984 and 1988 (Fig. 4B).

Drift patterns and the survival success of larvae through 18-mm SL differed among the four model scenarios that simulated the advection of larvae with and without vertical migration and included long-term changes in prey abundance and composition (Fig. 5A–D). For example, lower ambient temperatures at the beginning of the time series were associated with longer drift durations, larger drift distances, relatively high larval dispersal, and a relatively small fraction of larval survivors remaining in the deep basin (Fig. 5A). During the period when the probability of larval survival was extremely low (1984–1988) most of the survivors tended to be transported toward northern coastal environments (Fig. 5B). Similar to patterns obtained at the beginning of the time series, a more widespread distribution of larvae was also obtained from 1989 to 1994, a period of high temperatures but only average prey availability (Fig. 5C). Finally, during the most recent years, the distribution of survivors was less widespread because of relatively short drift durations (time to 18 mm) caused by high temperatures and above-average optimal prey availability (Fig. 5D). In general, larval dispersal was more widespread in scenario 6 model runs including daily vertical migration since larvae spent more time in cold water masses (during the day) resulting in longer drift durations and larger drift distances despite experiencing current velocities at mid-depth that were lower than those in layer directly below or above (within the wind-induced mixed layer).

Generally, the probability of survival of sprat larvae was markedly higher in the 1990s compared to the 1980s. First, the observed change in the main depth of occurrence of larvae (from deeper to upper water layers) simultaneously led to higher growth potential due to an increase in ambient temperature. Second, because of this change in larval behavior, higher survival rates resulted from the strong increase of the *Acartia* spp. biomass during the 1990s. However, improved larval growth conditions due to an increase in prey availability was particularly evident for individuals born earlier in the spawning season. In contrast, the main occurrence of larval sprat in the upper water layers was less beneficial if one was looking at later spawned individuals.

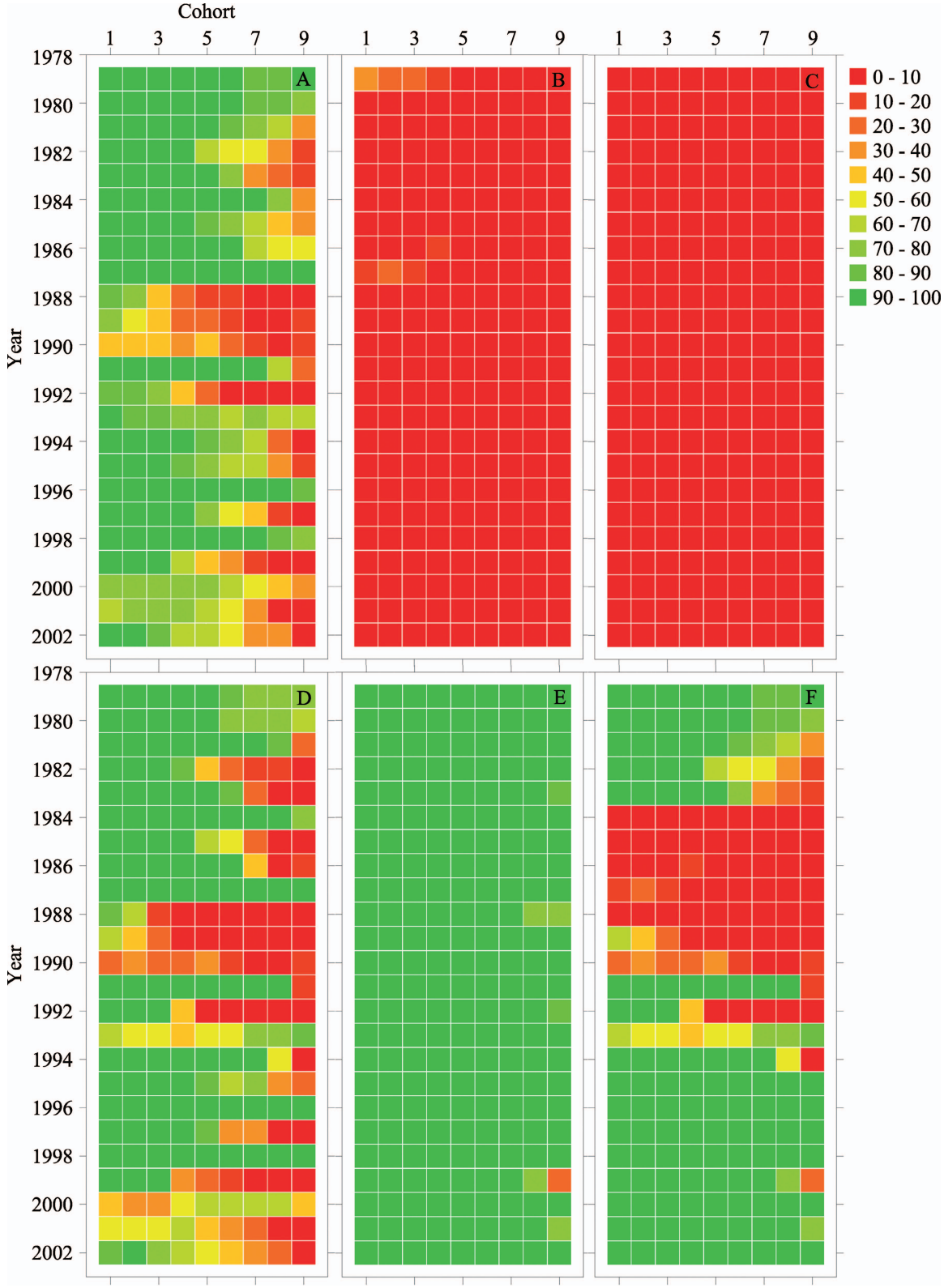

Fig. 3. Survival probability of early Baltic larval sprat in five different scenarios of larval vertical migration (VM) and/or copepod (*Pseudocalanus acuspus* and *Acartia* spp.) relative abundance combinations (A) scenario 1: VM, Pseudo 150%, Acartia 100%; (B) scenario 2: VM, Pseudo 100%, Acartia 100%; (C) scenario 3: VM, Pseudo 50%, Acartia 100%; (D) scenario 4: no VM, Pseudo 50%, Acartia 100%; (E) scenario 5: no VM, Pseudo 50%, Acartia 150%; and (F) scenario 6, composition of scenarios 1, 2, 4, and 5 (for details, *see* text).

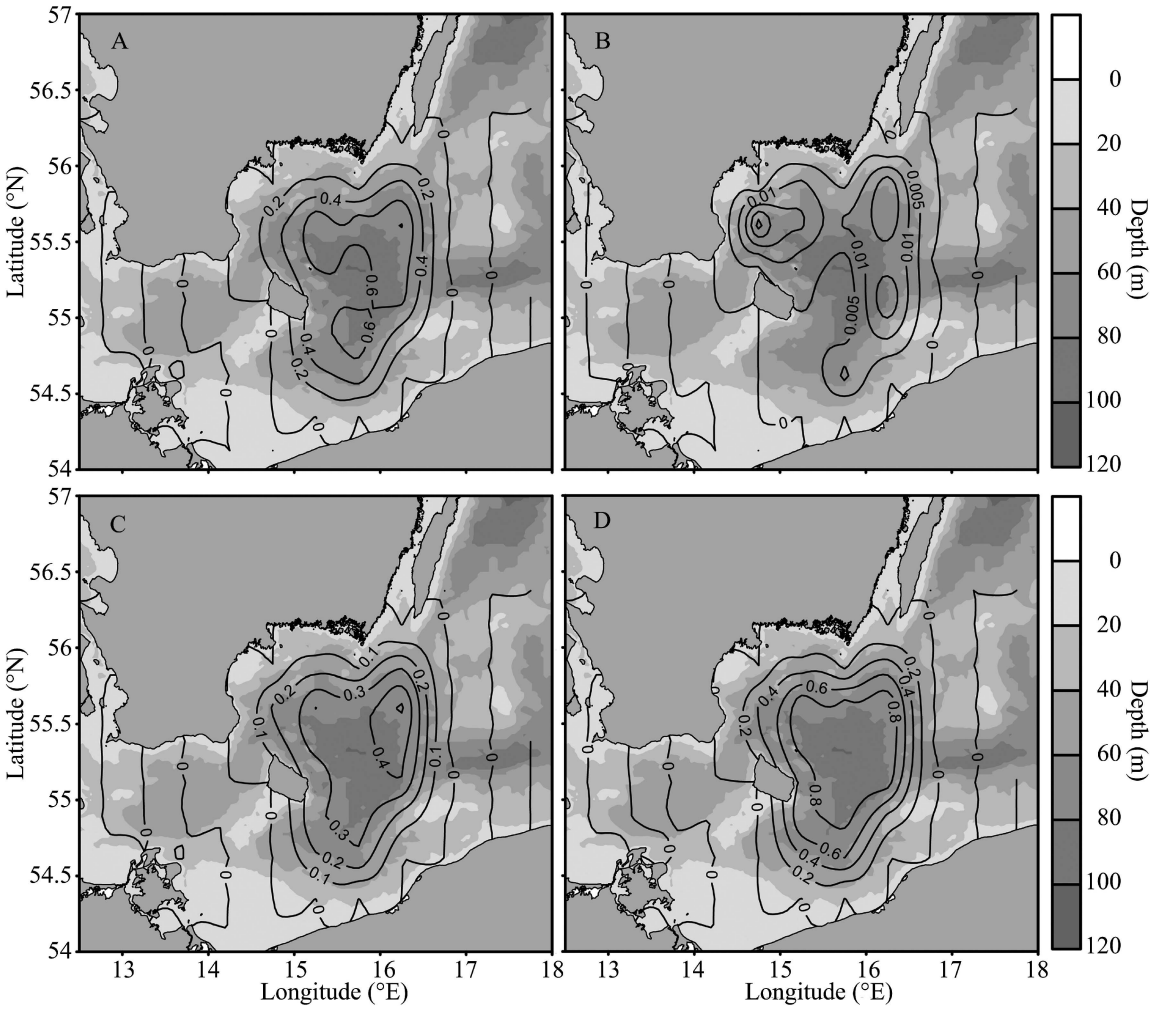

Fig. 4. Average horizontal distribution of mean larval survival probability in the Bornholm Basin according to larval release positions: (A) 1979–1983, scenario 1; (B) 1984–1988, scenario 2; (C) 1989–1994, scenario 4; and (D) 1995–2002, scenario 5.

Comparison of recruitment and annual larval survival of Baltic sprat—A weak yet statistically significant ($p < 0.05$) linear correlation ($r = 0.39$) was observed between simulated (scenario 6, annually averaged) and observed recruitment of Baltic sprat obtained from a Baltic Sea multispecies assessment model (Fig. 6). Between 1986 and 1990, both the relative annual larval survival rates and the recruitment of Baltic sprat were comparably low. The trend of increasing survival of offspring observed in the recruitment time series is also reflected in the model results. The relative weak correlation between modeled larval survival and observed recruitment was due to a much higher variability in larval survival compared to recruitment.

Discussion

Mechanistic understanding of long-term changes in marine systems—Although correlations between physical environmental changes and long-term changes in ecosystems have routinely been identified, the specific, underlying mechanisms are usually not resolved. Mechanistic understanding of marine ecosystem responses to long-term changes in climate forcing are often difficult to reveal because of (1) the simultaneous action of a suite of different and counteracting physical factors, (2) sensitivity of the ecosystem to the seasonal timing of the anomalous physical forcing, and/or (3) intrinsic ecosystem variability generated on climate time scales. However, temporal changes in zooplankton species abundance anomalies and composition appear to be sensitive indicators of changes in water mass characteristics and may be key elements in marine ecosystem changes.

In this study, we combined biophysical modeling and long-term field data to link climate-forced changes in abiotic (temperature and ocean currents) and biotic (prey composition and abundance) factors to changes in the survival of larval sprat in the Bornholm Basin. The effect of climate on the Baltic Sea ecosystem has been previously described by correlating phase changes in the North Atlantic Oscillation (NAO) to large-scale changes in plankton and fish (Hänninen et al. 2000). The present study defines the "mediator chain" linking changes in

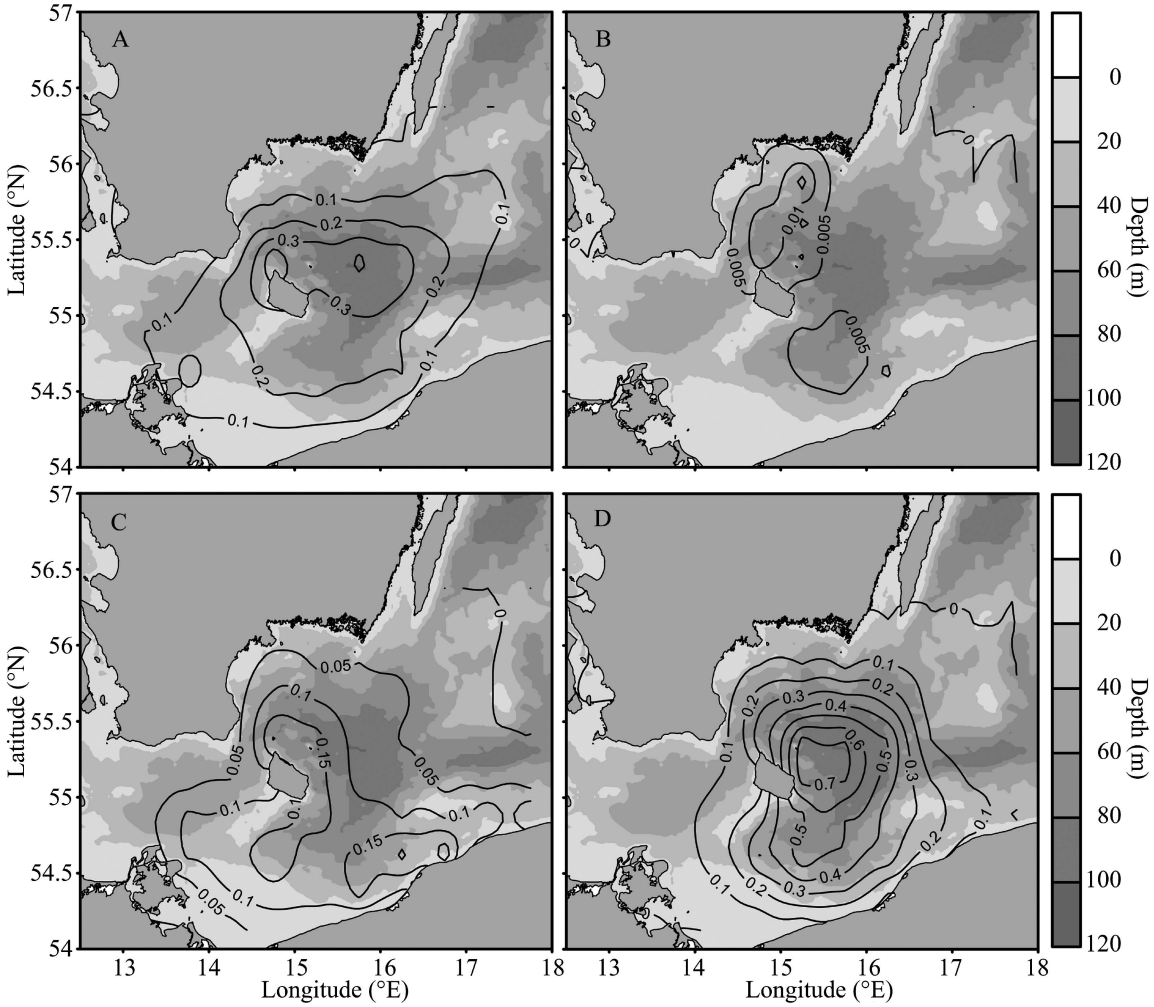

Fig. 5. Average horizontal distribution of mean larval survival probability in the Bornholm Basin according to final larval positions: (A) 1979–1983, scenario 1; (B) 1984–1988, scenario 2; (C) 1989–1994, scenario 4; and (D) 1995–2002, scenario 5.

large-scale climate indices such as the NAO to submesoscale effects and the response of a key secondary consumer in the Baltic Sea food web.

According to our IBM scenarios, the mixed water layer (0–40-m depth) generally supported high rates of growth and hence survival of larval sprat in the Bornholm Basin of the Baltic Sea. This range in depths coincides with the general vertical distribution of larvae obtained from field samples in the Baltic during the past two to three decades. Larger larvae were found at shallower depths levels, whereas only the smallest larvae were found in the deeper layers. Wieland and Zuzarte (1991) found a deep maximum of small larvae (< 6 mm) occurring at 70–75 m and older larvae (up to 19 mm) predominantly in the upper 45 m. These differences in the vertical distribution of larvae with ontogeny suggest that most larvae hatch at deeper layers and then migrate to the upper layers, where they remain until at least the juvenile phase (Voss et al. 2007). Besides ontogenetic changes in depth preference, vertical positions chosen by larval fish may be due to behavioral response to environmental gradients (Vikebø et al. 2007). Strong selection pressures on habitat selection in larval sprat could be expected since the pelagic environment in the Baltic Sea is characterized by strong vertical gradients of abiotic as well as biotic variables that affect the growth of sprat larvae (i.e., temperature, prey concentrations, and the probability of being advected into unfavorable areas for

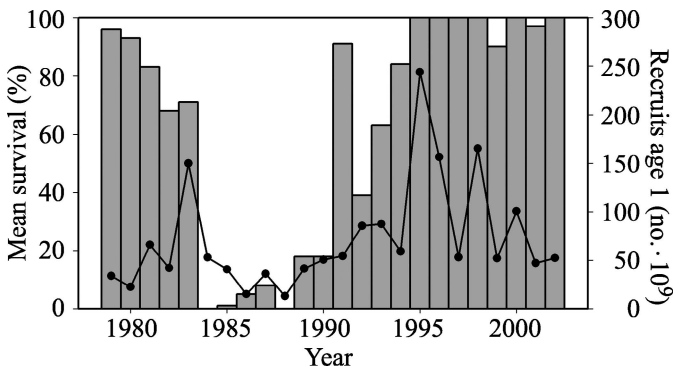

Fig. 6. Time series of mean annual larval survival (bars) vs. recruitment of Baltic sprat (dots and line).

survival). Our analyses revealed the effects of seasonal as well as long-term trends in temperature, light (not shown), and zooplankton species abundance and distribution on the survival of sprat larvae. Our scenarios were also able to explore changes in optimal depth ranges and foraging strategies during early ontogeny.

Depth-dependent dispersion and survival of Baltic sprat early life stages—Because of differences in vertical distribution, marine larval fish dwelling in layered current systems might be advected in different directions at different speeds (Vikebø et al. 2007). For example, ocean circulation models suggest that passively drifting young larvae released at depths only 10 m apart may metamorphose into juveniles many weeks later at very different locations (Vikebø et al. 2005). Indeed, a previous Lagrangian drift study performed on sprat in the deep central basins of the Baltic Sea (Bornholm Basin, Gdansk Deep, and Gotland Basin) indicated markedly different drift trajectories for larvae with and without diurnal vertical migration (Hinrichsen et al. 2005). In those scenarios, the number of sprat retained in the deep basins was generally higher if the larvae were allowed to move vertically since current velocities at mid-depth were lower than in the layers directly below or within the wind-induced mixed layer. Moreover, the weaker mid-depth currents could be of different direction than the higher velocity currents close to the surface. For larval sprat, transport is determined primarily by the wind-driven circulation of the Baltic Sea. Wind stress acting at the sea surface results in Ekman transport at a right angle to the wind in the near-surface layers, with coastal jets produced in direction of the wind along both coasts of the basin. The Ekman flow is compensated by a mainly topographically steered return flow in the central interior of the basins (Krauss and Brügge 1991), which is generally in a direction opposite to the prevailing winds. Because of lower current velocities at mid-depth, the mean final bottom depth of the larval cohorts released at those depths was higher compared to larval cohorts that were exclusively exposed to the higher directly wind-driven current speeds close to the sea surface (Hinrichsen et al. 2005).

Our modeling results shed light on a potentially strong mechanism linking environmental variability and recruitment success in Baltic Sea sprat. Köster et al. (2003) reported significant relationships between covariances of abundance estimates between early and late egg stages and between the late larval and the early juvenile stages but no significant relationship between year-class strength and larval abundance. These findings suggested that processes acting during the late larval and early juvenile phase were critical to year-class success, a finding recently shared by Baumann et al. (2006). Our study suggests that climate affects Baltic larval sprat both directly (in terms of temperature) and indirectly (via changes to populations of specific prey species). More specifically, our results suggest that the dramatic increase in sprat spawning biomass since the 1980s also could be potentially due to beneficial changes in the vertical distribution pattern of (and environments experienced by) early sprat larvae. The observed strong recruitment variability in the 1990s could be explained by larval advection and density-dependent processes acting on juvenile stages in coastal areas (Baumann et al. 2006). Markedly higher survival of early larval sprat in the past decade could be due to prey-driven changes in their foraging behavior. A lack of diel vertical migration resulted in larvae spending more time within more optimal ambient temperatures (warmer) and feeding conditions (higher prey concentrations) as opposed to diel migrators that foraged during the day in suboptimal (cooler) temperatures at lower prey concentrations. Our model results suggested that survival was impossible for individuals who performed diel vertical migration after the reduction of *P. acuspes*. Consequently, the shift in behavior resulted in an increased susceptibility of larvae to unfavorable transport by wind-driven surface currents. Thus, our model results suggest a plausible mechanism acting during the late larval and early juvenile period to explain the increase in both Baltic sprat productivity (in the absence of strong predation pressure) and density-dependent recruitment variability (due to unfavorable surface drift).

Our study must be seen as an initial approach and an example of how simple, yet strategic trade-offs leading to different patterns of larval vertical distribution can be used in combination with a circulation model to study differences in larval feeding success, growth, and potential survival. Fiksen et al. (2007) stated that larval fish simply execute genetically preprogrammed responses to internal states or external stimuli. From our analysis, it could not be ultimately clarified whether the observed higher survival probability of larval sprat during the past decade was due to a change in behavior. It is possible that minor fractions of larvae, which occurred predominantly in upper water layers also during the 1980s, were the only successful contributors to recruitment to the adult population as the feeding environment underwent the observed regime shift. Naturally, our study cannot address whether selection of specific behavioral phenotypes was acting on this Baltic sprat population in previous decades. Although it is possible that sprat subpopulations may have formed because of the limited connectivity among groups of sprat spawning in distinct Baltic areas (Hinrichsen et al. 2005), possible genetic and/or behavioral differences within or between spawning populations remains an interesting albeit unstudied phenomenon. Evolutionary effects on population distributions as well as the potential for genetic differences between different fish stock components can be obtained only by analysis of long-term average pattern of juvenile distributions if there is evidence for active or passive mixing of the spawning products of different adult stock components.

Several topics were not addressed in our study but are good candidates for future work. First, a more thorough analysis of spatial (horizontal) differences in survival characteristics of larvae is needed. Our spatial analysis of the results from scenario 6 indicated that different spawning (larval release) areas had different survival probabilities and that those probabilities were not constant throughout the years simulated (1979–2003). In our

relatively simple approach we have analyzed differences in survival rates among individuals as a function of ambient temperature and mean zooplankton abundance. In our study we did not examine the effect of small- to medium-scale variability in prey fields on larval survival. However, high variability is often observed in growth and condition of larval fish captured at the same station, which may reflect large differences in realized feeding rates due to small-scale prey patchiness (Young et al. 2009). Although observations that allow the construction and utilization of small-scale prey patches within larval fish IBMs are often unavailable, incorporating patch dynamics (using statistical approaches) are envisaged in the future whereby models offering higher spatial resolution may increase our knowledge of relevant processes in nature.

Climate-driven ecosystem changes and sprat recruitment—During the 1990s, sprat recruitment per unit spawner in the central Baltic Sea increased because of increasing water temperatures, which increased the survival probability of sprat eggs and caused a beneficial shift in the dominant copepod species from *P. acuspes* to *Acartia* spp. (Möllmann et al. 2000). Prior to that period, the Baltic Sea experienced more regular inflow events of North Sea water, which maintained higher salinity and oxygen levels and promoted the persistence of large *P. acuspes* and cod populations. High populations of Baltic cod exerted considerable predatory control of the sprat population (Möllmann et al. 2009) until their collapse (due to climate and overfishing) in the late 1980s. The loss of Baltic cod induced cascading effects in the Baltic Sea food web (Casini et al. 2009). For example, increased populations of Baltic sprat could then exert top-down control of *P. acuspes* populations (Möllmann et al. 2008). leading to a change of the Baltic Sea ecosystem, which is now dominated by sprat and *Acartia* spp. This trophic cascade has now established a stabilizing prey-to-predator system in the Baltic, which is now dominated by sprat and *Acartia* spp. and is likely to remain so in the future (Möllmann et al. 2009). In this context, it seems very likely that the change in vertical migration behavior of larval Baltic sprat examined in the present study could be considered a secondary effect and one that helps stabilize the current food web structure by maintaining sprat at high population sizes. Projected increased water temperatures in the Baltic will be a second factor maintaining the current trophodynamic situation by favoring *Acartia* spp. Thus, environmental projections for the Baltic suggest that it is highly unlikely that abiotic and biotic factors will change to destabilize the sprat-dominated ecosystem in the 21st century.

The main purpose of the present study was to identify links between changes in climate, larval behavior, and the probability of survival of Baltic sprat larvae. Year-class strength in Baltic sprat can be strongly affected by environmental factors acting during the late larval and early juvenile stages (Baumann et al. 2006; Voss et al. 2006). From this study, a weak but significant correlation between recruitment and annual larval survival probability was obtained. However, it should be noted that our model approach was not designed to yield a better prediction of Baltic sprat recruitment. The latter would entail combining more detailed information on larval drift (Baumann et al. 2006), spawning stock biomass, and larval survival probability (this study), which was not possible here since (1) the recruitment time series was based on the aggregate sprat stock (Bornholm Basin, Gotland Basin, and Gdansk Deep), while our analysis was performed only on larvae from one major spawning area (Bornholm Basin); (2) based on our two measurement periods (late 1980s and early 2000s), we are unable to ascertain the time course of change in Baltic sprat vertical distribution; and (3) converting from relative survival (this study) to absolute survival requires highly temporally and spatially resolved data on prey fields and early larval stage or late egg stage abundance that are currently unavailable.

Acknowledgments

This study has been carried out with financial support from the German Federal Ministry for Education and Research within the Global Ocean Ecosystem Dynamics (GLOBEC) project and from the European Communities as a contribution to the FP6 Specific Targeted Research Projects 022717, Understanding the Mechanisms of Stock Recovery (UNCOVER), and 044133, Resolving Climatic Impacts on fish stocks (RECLAIM). This article does not necessarily reflect the views of the Commission.

References

Bailey, K. M., and E. D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. **25:** 1–67, doi:10.1016/S0065-2881(08)60187-X

Barz, K., and H. J. Hirche. 2005. Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). Mar. Biol. **147:** 465–476, doi:10.1007/s00227-005-1572-2

Baumann, H., H.-H. Hinrichsen, C. Möllmann, F. W. Köster, A. M. Malzahn, and A. Temming. 2006. Recruitment variability in Baltic sprat, *Sprattus sprattus*, is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. Can. J. Fish. Aquat. Sci. **63:** 2191–2201, doi:10.1139/F06-112

Bryan, K. 1969. A numerical method for the study of the circulation of the world ocean. J. Phys. Oceanogr. **15:** 1312–1324.

Casini, M., and others. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proc. Natl. Acad. Sci. USA **106:** 197–202, doi:10.1073/pnas.0806649105

Daewel, U., M. A. Peck, W. Kühn, M. A. St. John, I. Alekseeva, and C. Schrum. 2008. Coupling ecosystem and individual-based models to simulate the influence of environmental variability on potential growth and survival of larval sprat (*Sprattus sprattus* L.) in the North Sea. Fish. Oceanogr. **17:** 333–351, doi:10.1111/j.1365-2419.2008.00482.x

Dickmann, M., C. Möllmann, and R. Voss. 2006. Feeding ecology of Central Baltic sprat (*Sprattus sprattus* L.) larvae in relation to zooplankton dynamics—implications for survival. Mar. Ecol. Prog. Ser. **342:** 277–289, doi:10.3354/meps342277

Fiksen, Ø., C. Jørgensen, T. Kristiansen, F. Vikebø, and G. Huse. 2007. Linking behavioural ecology and oceanography: Larval behaviour determines growth, mortality and dispersion. Mar. Ecol. Prog. Ser. **347:** 195–205, doi:10.3354/meps06978

Fuiman, L. A., and J. C. Gamble. 1988. Predation by Atlantic herring, sprat and sandeels on herring larvae in large enclosures. Mar. Ecol. Prog. Ser. **44:** 1–6, doi:10.3354/meps044001

Hänninen, J., I. Vuorinen, and P. Hjelt. 2000. Climate factors in Atlantic control the oceanographic and ecological changes in the Baltic Sea. Limnol. Oceanogr. **45:** 703–710.

Haslob, H., and others. 2007. Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. Mar. Ecol. Prog. Ser. **349:** 303–306, doi:10.3354/meps07283

Hernroth, L. 1985. Recommendations on methods for marine biological studies in the Baltic Sea: Mesozooplankton biomass assessment. The Baltic Marine Biologist **10:** 1–32.

Hinrichsen, H.-H., G. Kraus, R. Voss, D. Stepputtis, and H. Baumann. 2005. The general distribution of pattern and mixing probability of Baltic sprat juvenile populations. J. Mar. Syst. **58:** 52–66, doi:10.1016/j.jmarsys.2005.06.003

———, C. Möllmann, R. Voss, F. W. Köster, and G. Kornilovs. 2002. Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. Can. J. Fish. Aquat. Sci. **59:** 1858–1873, doi:10.1139/f02-149

Killworth, P. D., D. Stainforth, D. J. Webbs, and S. M. Paterson. 1991. The development of a free-surface Bryan-Cox-Semtner ocean model. J. Phys. Oceanogr. **21:** 1333–1348, doi:10.1175/1520-0485(1991)021<1333:TDOAFS>2.0.CO;2

Kiørboe, T., P. Munk, and K. Richardson. 1987. Respiration and growth of larval herring *Clupea harengus*: Relation between specific dynamic action and growth efficiency. Mar. Ecol. Prog. Ser. **40:** 1–10, doi:10.3354/meps040001

Köster, F. W., H.-H. Hinrichsen, M. A. St. John, D. Schnack, B. R. Mackenzie, J. Tomkiewicz, and M. Plikshs. 2001. Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. Can. J. Fish. Aquat. Sci. **58:** 973–984.

———, and others. 2003. Fish stock development in the central Baltic Sea (1974–1999) in relation to variability in the environment. ICES Mar. Sci. Symp. **219:** 294–306.

Krauss, W., and B. Brügge. 1991. Wind-produced water exchange between the deep basins of the Baltic Sea. J. Phys. Oceanogr. **11:** 415–433, doi:10.1175/1520-0485(1981)011<0415:TEOAT>2.0.CO;2

Leggett, W. C., and E. Deblois. 1994. Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? Neth. J. Sea Res. **32:** 119–134, doi:10.1016/0077-7579(94)90036-1

Lehmann, A., and H.-H. Hinrichsen. 2000. On the thermohaline variability of the Baltic Sea. J. Mar. Syst. **25:** 333–357, doi:10.1016/S0924-7963(00)00026-9

———, W. Krauß, and H.-H. Hinrichsen. 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. Tellus **54:** 299–316, doi:10.1034/j.1600-0870.2002.00289.x

Letcher, B. H., J. A. Rice, L. B. Crowder, and K. A. Rose. 1996. Variability in survival of larval fish: Disentangling components with a generalized individual-based model. Can. J. Fish. Aquat. Sci. **53:** 787–801, doi:10.1139/cjfas-53-4-787

Möllmann, C., R. Diekmann, B. Müller-Karulis, G. Kornilovs, M. Plikshs, and P. Axe. 2009. Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: A discontinuous regime shift in the Central Baltic Sea. Glob. Change Biol. **15:** 1377–1393, doi:10.1111/j.1365-2486.2008.01814.x

———, G. Kornilovs, and L. Sidrevics. 2000. Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. J. Plankton Res. **22:** 2015–2038, doi:10.1093/plankt/22.11.2015

———, and F. W. Köster. 1999. Food consumption by clupeids in the Central Baltic: Evidence for top-down control? ICES J. Mar. Sci. **56:** 100–113, doi:10.1006/jmsc.1999.0630

———, and ———. 2002. Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. J. Plankton Res. **24:** 959–977, doi:10.1093/plankt/24.10.959

———, B. Müller-Karulis, G. Kornilovs, and M. A. St. John. 2008. Effects of climate and overfishing on zooplankton dynamics and ecosystem structure—regime shifts, trophic cascade and feedback loops in a simple ecosystem. ICES J. Mar. Sci. **65:** 302–310, doi:10.1093/icesjms/fsm197

Munk, P. 1992. Foraging behaviour and prey size spectra of larval herring *Clupea harengus*. Mar. Ecol. Prog. Ser. **80:** 149–158, doi:10.3354/meps080149

———, and T. Kiørboe. 1985. Feeding behaviour and swimming activity of larval herring (*Clupea harengus* L.) in relation to density of copepod nauplii. Mar. Ecol. Prog. Ser. **24:** 15–21, doi:10.3354/meps024015

Nissling, A., A. Müller, and H.-H. Hinrichsen. 2003. Specific gravity and vertical distribution of sprat (*Sprattus sprattus*) eggs in the Baltic Sea. J. Fish Biol. **63:** 280–299, doi:10.1046/j.1095-8649.2003.00139.x

Parmanne, R., O. Rechlin, and B. Sjöstrand. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana **10:** 29–59.

Peck, M. A., L. J. Buckley, and D. A. Bengtson. 2006. Effects of temperature and body size on the swimming speed of larval and juvenile Atlantic cod (*Gadus morhua*): Implications for individual-based modelling. Environ. Biol. Fishes **75:** 419–429, doi:10.1007/s10641-006-0031-3

———, C. Clemmesen, and J.-P. Herrmann. 2005. Ontogenic changes in the allometric scaling of the mass and length relationship in *Sprattus sprattus*. J. Fish. Biol. **66:** 882–887, doi:10.1111/j.0022-1112.2005.00651.x

Ré, P., and E. Gonçalves. 1993. Growth of *Sprattus sprattus* larvae in the German Bight (North Sea) as inferred from otolith microstructure. Mar. Ecol. Prog. Ser. **96:** 139–145, doi:10.3354/meps096139

Schmidt, J. 2006. Small and meso-scale distribution patterns of key copepod species in the Central Baltic Sea and their relevance for larval fish survival. Ph.D. thesis. Univ. of Kiel.

STORE. 2003. Environmental and fisheries influences on fish stock recruitment in the Baltic Sea. Final Report, EU Project FAIR 98 3959.

Vikebø, F., C. Jørgensen, T. Kristiansen, and Ø. Fiksen. 2007. Drift, growth, and survival of larval Northeast Atlantic cod with simple rules of behaviour. Mar. Ecol. Prog. Ser. **347:** 207–219, doi:10.3354/meps06979

———, S. Sundby, B. Adlandsvik, and Ø. Fiksen. 2005. The combined effect of transport and temperature on distribution and growth of larvae and pelagic juveniles of Arcto-Norwegian cod. ICES J. Mar. Sci. **62:** 1375–1386, doi:10.1016/j.icesjms.2005.05.017

Voss, R., C. Clemmesen, H. Baumann, and H.-H. Hinrichsen. 2006. Baltic sprat larvae: Coupling food availability, larval condition and survival. Mar. Ecol. Prog. Ser. **308:** 243–254, doi:10.3354/meps308243

———, F. W. Köster, and M. Dickmann. 2003. Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fish. Res. **63:** 97–111.

———, J. O. Schmidt, and D. Schnack. 2007. Vertical distribution of Baltic sprat larvae: Changes in patterns of diel migration? ICES J. Mar. Sci. **64:** 956–962, doi:10.1093/icesjms/fsm068

Vuorinen, I., J. Hänninen, M. Vitasalo, U. Helminen, and H. Kuosa. 1998. Proportion of copepod biomass declines with decreasing salinity in the Baltic Sea. ICES J. Mar. Sci. **55:** 767–774, doi:10.1006/jmsc.1998.0398

Walton, W. E., N. G. Hairston, and J. K. Wetterer. 1992. Growth-related constrains on diet selection by sunfish. Ecology **73:** 429–437, doi:10.2307/1940750

Wieland, K., and F. Zuzarte. 1991. Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987–1990. ICES C.M.1991/J, 37.

Young, K. V., J. F. Dower, and P. Pepin. 2009. A hierarchical analysis of the spatial distribution of larval fish prey. J. Plankton Res. **31:** 687–700, doi:10.1093/plankt/fbp017

Associate editor: Michael R. Landry

Received: 30 July 2009
Accepted: 15 February 2010
Amended: 16 March 2010